# FEEDING RATE OF CALANUS FINMARCHICUS IN RELATION TO ENVIRONMENTAL CONDITIONS [1]

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## OBJECTIVES

The amount of food available to a plankton-feeding animal is determined by the concentration of suitable food material in the water, and by the rate of the animal's feeding activity. The calanoid copepods, like many other zoöplanktonts, are generally considered to feed by filtering out particles from a current of water generated by the animals (Cannon, 1928). By determining the number of food organisms removed by an animal from a suspension of known concentration, the volume of water which has been filtered clear of the organisms can be calculated and, if the chemical composition of the organisms be known, the amount of nutriment made available to the animal may be estimated. Preliminary measurements of the filtering rate of *Calanus finmarchicus* have been reported by Fuller and Clarke (1936). Further investigation of changes in the feeding rate induced by varying environmental factors of ecological importance was expected to yield information useful in the quantitative study of aquatic food cycles. Diatom concentration, light and temperature were expected to be variable factors in the sea and were chosen for study.

## METHODS

In the experiments here reported the rate of feeding of the copepod *Calanus finmarchicus*, collected in Vineyard Sound near the whistle buoy, was measured in a suspension of the diatom *Nitzschia closterium* (Plymouth strain). It seems probable that *Nitzschia* is a suitable food for *Calanus*, as Crawshay (1913–15) kept individual copepods alive for as long as 80 days in persistent cultures of this diatom. Allen and Nelson (1910, p. 470) reared *Calanus* from eggs to copepodid stages in a mixed culture in which *Nitzschia* was predominant.

Three stage V *Calanus* were placed in 15 cc. of sea water containing a known concentration of diatoms. Changes in concentration were followed for two to four days, counts being made in a hemacytometer.

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A series of counts on successive samples showed fair agreement with the theoretical Poisson distribution. The small excess variation found is attributed to the difficulty of shaking the diatoms to obtain even distribution without injuring the copepods. Enough diatoms were counted for each sample to give a result statistically valid to between 5 and 10 per cent. Under the experimental conditions this is the maximum precision obtainable. In these experiments a counting error of 10 per cent causes a discrepancy of about 30 per cent in the estimation of the filtering rate. Obviously only large variations can be satisfactorily studied.

## TABLE I

*Feeding rate at different diatom concentrations*

| Expt. No. | Date begun | Cells per cc. | | Duration | $W_{24}$ | $\Delta N_{24}$ |
|---|---|---|---|---|---|---|
| | | $C_1$ | $C_2$ | | | |
| | | | | *hours* | *cc.* | |
| 47 | Aug. 18 | 1,875 | 1,140 | 42 | 1.32 | 2,100 |
| 48 | Aug. 18 | 1,875 | 1,155 | 42 | 1.28 | 2,060 |
| 63 | Aug. 23 | 19,000 | 15,400 | 38 | .66 | 11,400 |
| 64 | Aug. 23 | 19,000 | 13,100 | 38 | 1.17 | 16,100 |
| 14 | July 9 | 64,700 | 27,000 | 81 | 1.30 | 55,000 |
| 15 | July 9 | 64,700 | 27,700 | 81 | 1.25 | 55,000 |
| 71 | Aug. 26 | 190,000 | 147,000 | 38 | .81 | 136,000 |
| 72 | Aug. 26 | 200,000 | 133,000 | 38 | 1.29 | 212,000 |
| 11 | July 3 | 335,000 | 86,000 | 84 | 1.61 | 356,000 |
| 10 | July 3 | 375,000 | 220,000 | 84 | .43 | 221,000 |
| 8 | June 29 | 390,000 | 130,000 | 84 | 1.32 | 371,000 |
| 7 | June 29 | 410,000 | 230,000 | 84 | .60 | 256,000 |
| | | | | Average | 1.09 | |

Calculation of the amount of water, $W_x$, swept free of diatoms by each copepod in $x$ hours was made by means of an equation derived as follows:

$$(1) \qquad dN = -dWC$$

$$(2) \qquad dC = dN/V$$

$$(3) \qquad dW = VdC/C$$

$$(4) \qquad W_x = V \ln C_1/C_2.$$

$N$ represents the number of diatoms per copepod; $V$ the volume of water per copepod; $C_1$ and $C_2$ respectively the concentrations of diatoms at the beginning and end of the period of $x$ hours.

The number of diatoms eaten in $x$ hours per copepod, $\Delta N_x$, is given

by the equation:

(5) $$\Delta N_x = V(C_1 - C_2).$$

Parallel control suspensions were always counted to determine whether the diatom numbers were varying independently. If a control changed greatly during the experimental period, the results of the corresponding experimental series were discarded. If the change was small, the final concentration of diatoms in the control was substituted for $C_1$ in equations (4) and (5). This substitution assumes that the diatoms in the experimental containers increased or decreased independently exactly as those in the control. This is, of course, only an approximation.

Observations were also made on the production of fecal pellets. Since these pellets vary greatly in size no quantitative relationship could be obtained between the number of diatoms ingested and the number of pellets ejected. However, the formation of these excreta was a useful check on the reduction of diatom numbers observed directly.

### Effect of Changing Diatom Concentration

Table I gives the results of experiments with different concentrations of diatoms. In the lowest concentration the diatoms were concentrated by the Nielsen-von Brand (1934) method before counting. These experiments were carried out at 13° C., and the animals were shielded from direct sunlight. The values for $W_{24}$ and $N_{24}$ in the table represent means over a period of several days. Diatom concentration often remains stationary for a day or more, thus indicating that feeding is not a continuous process. The maximum rate of filtration is higher than these values. The highest rate observed was in Experiment 11 where over a period of 14 hours $W$ equalled 2.87 cc. which would give a $W_{24}$ value of 4.9 cc. There appears to be no correlation between the concentration of food and the filtering rate. A comparison of the filtering rates of animals collected at different times during the summer yields no greater differences than a comparison of animals collected at the same time and used in parallel experiments (e.g. Nos. 10 and 11). The indication is that *Calanus*, though it sometimes does not feed actively, under otherwise constant conditions filters a definite volume of water per day, and obtains nutriment in direct proportion to the concentration of food particles.

### Effect of Light on Feeding Rate

In certain experiments there appeared to be a diurnal feeding rhythm, removal of diatoms taking place most rapidly at night. This

is in accord with the observation of Marshall (1924), who notes that *Calanus* captured by tow-net hauls in the early morning had full guts, while those caught later in the day often had no food in their alimentary tracts.    Figure 1 represents the course of two experiments (8 and 11) which show this rhythm.    It is not, however, an invariable
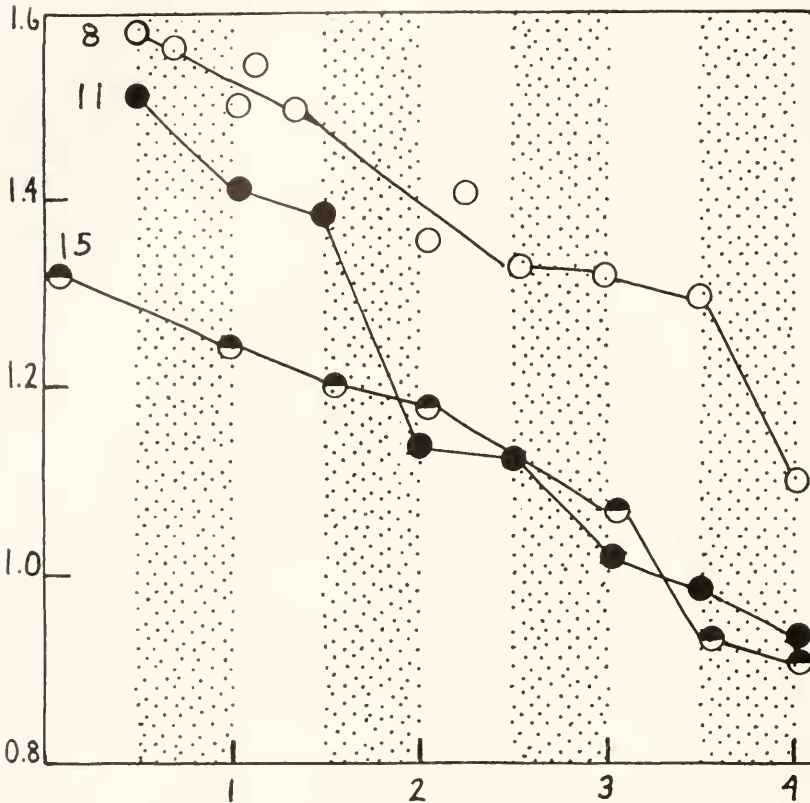


FIG. 1.   Diurnal feeding rhythm of *Calanus*.   Stippled areas represent hours between 8 P.M. and 8 A.M.   The scale of Experiment 15 is adjusted by adding 0.5 to logarithms of cell numbers.   Ordinates: *Logarithm-cells per 0.1 cu mm.*   Abcissæ: *Time in days.*

effect, as is shown by the course of Experiment 15, also shown in Fig. 1. Marshall likewise found that during the summer feeding occurred during the day as well as at night.

Experiments 26 and 32 differed from those reported above in being kept in darkness.   Table II summarizes the results of these two experiments.

TABLE II

*Feeding rate in dark*

| Expt. No. | Date begun | Cells per cc. | | Duration | $W_{24}$ | $N_{24}$ |
|---|---|---|---|---|---|---|
| | | $C_1$ | $C_2$ | | | |
| | | | | *hours* | *cc.* | |
| 26 | July 16 | 54,000 | 32,000 | 90 | .27 | 45,000 |
| | | | | 48* | .76* | |
| 32 | July 30 | 61,000 | 20,000 | 65 | 1.8 | 76,000 |

* Animals actually fed only during last 48 hours of experiment.    $W_{24}$ value calculated for this period.

The results do not differ significantly from the average given in Table I, although there are admittedly too few cases to permit a definite answer.    An attempt was made to study the effect of continuous light.    The animals did not feed during the two days they were observed, but they were old stock in poor condition, and no reliance should be placed on this observation.    Unfortunately it was impossible to collect more *Calanus* to make satisfactory experiments.

### Effect of Temperature on Feeding Rate

Experiments were carried out at 8° C. and at approximately 3° C. The latter temperature was not precisely controlled as the containers were placed in a refrigerator in general laboratory use.    Both series were kept in the dark.

Feeding is much slower at 3° but still goes on with the formation of small compact fecal pellets.    The very low filtering rates observed in Experiments 75 to 79 may be explained by the fact that the animals used were collected late in the season when the *Calanus* population was receding rapidly, and had perhaps stopped eating.    The filtering rate in Experiment 80, in which the same stock was used, is seen to be much slower than that in Experiments 55 and 56.    The high value for $W_{24}$ in the latter experiments seems to indicate that 8° C. is somewhat more favorable for feeding than 13°.    Excluding Experiments 75 to 80, the average values of $W_{24}$ at 3°, 8° and 13° are respectively, 0.35, 2.83 and 1.09 cc.

### Organic Nitrogen Content of Nitzschia and of Plankton

Through the kindness of Dr. Theodor von Brand, an analysis of the organic nitrogen content of *Nitzschia* was made by the method he has developed for small amounts of plankton (von Brand, 1935). *Nitzschia* contains 0.9 microgram of nitrogen per million cells.    Assuming the carbon-nitrogen ratio in this diatom to be equal to that

generally found in marine phytoplankton, approximately 8 : 1, we have 7.2 micrograms of carbon per million cells. Analysis of the fecal pellets of *Calanus* fed on *Nitzschia* showed that 0.55 microgram of nitrogen appeared in the feces for each million cells ingested. Roughly, about half the organic nitrogen was retained by the copepods.

Marshall, Nicholls and Orr (1935) have calculated from measurements of oxygen consumption the daily nutritive requirement of a stage V *Calanus* in summer as equal to 13 micrograms of carbohydrate. Assuming all the nitrogen of *Nitzschia* to be in protein, and the excess carbon to be in fat, one may calculate the number of cells which would supply an equal amount of energy. If the protein is assumed to contain 16 per cent nitrogen and 50 per cent carbon; the fat to contain 75 per cent carbon, we have:

TABLE III

*Effect of temperature on feeding rate*

| Expt. No. | Temp. | Date begun | Cells per cc. | | Dura-tion | $W_{24}$ | $N_{24}$ |
|---|---|---|---|---|---|---|---|
| | | | $C_1$ | $C_2$ | | | |
| | ° C. | | | | hours | cc. | |
| 42 | 3° | Aug. 18 | 263,000 | 215,000 | 90 | .38 | 64,000 |
| 43 | 3° | Aug. 18 | 263,000 | 223,000 | 90 | .32 | 53,000 |
| 55 | 8° | Aug. 22 | 85,500 | 30,000 | 42 | 2.88 | 159,000 |
| 56 | 8° | Aug. 22 | 85,500 | 31,000 | 42 | 2.78 | 156,000 |
| 80 | 8° | Aug. 31 | 24,000 | 14,000 | 65 | .98 | 18,500 |
| (75, 76) | | Aug. 31 | | | 85 | .00 | 0 |
| (79) | 8° | | | | | | |

$$0.9 \times 0.16 = 5.62 \ \gamma \ \text{protein containing } 2.8 \ \gamma \ C.$$
$$7.2 - 2.8 = 4.4 \ \ \gamma \ C \ \text{in fat}$$
$$4.4 \times 0.75 = 5.87 \ \gamma \ \text{fat.}$$

Proteins and carbohydrates have equal energy values per unit of weight. Fat has 2.25 as great an energy content as carbohydrate. Calculating fat and protein in terms of carbohydrate, we obtain:

$$5.87 \times 2.25 = 13.2$$
$$\underline{\phantom{5.87 \times 2.25 = 1}5.6}$$
$$18.8 \ \gamma \cdot \text{weight of carbohydrate equivalent in}$$
energy content to a million *Nitzschia* cells.

$$\frac{13}{18.8} \times 1,000,000 = 690,000 \ \text{number of } \textit{Nitzschia} \ \text{cells which would}$$
contain theoretical food requirement.

The maximum amount of water filtered per day ($W_{24}$) in any experiment was 2.88 cc. A concentration of 240,000 cells per cc. would be required if *Calanus* is to obtain its theoretical food requirement from this volume of water, even if all the organic matter is utilized. Probably this value should be doubled since only half the nitrogenous organic matter appears to be assimilated. In any case this is a much higher concentration of phytoplankton than ever occurs in nature, but since the size of phytoplankton cells varies so greatly, comparisons based on cell numbers are worthless. It is, however, possible to determine the organic nitrogen content of the particulate matter in sea water, and to compare this with the food requirements of *Calanus*. Table IV summarizes the results of two sets of analyses by Dr. von Brand of the particulate matter suspended in Vineyard Sound water. All macroscopically visible organisms were removed

TABLE IV

*Organic N in particulate matter in Vineyard Sound water*

| Date | Depth | Temperature | N |
|---|---|---|---|
| | *meters* | *° C.* | *per liter micrograms* |
| July 2 | 0 | 17.8 | 15 |
| | 15 | 13.5 | 27 |
| | 30 | 9.1 | 13 |
| August 14 | 0 | 20.0 | 38 |
| | 15 | 18.0 | 42 |
| | 30 | 12.0 | 19 |

from the August 14 samples before analysis. This was not done for the July 2 samples.

The maximum value found was $42\gamma$N per liter, a nitrogen concentration equal to that of a *Nitzschia* culture containing 46,700 cells per cc. This is so far above the average number of diatoms per cc. in Vineyard Sound—the figure is probably close to 100—that, even allowing for the fact that one large cell is the equivalent of many *Nitzschia*, it appears probable that the major portion of the particulate matter at this station was not in the form of diatoms. The remainder, detritus or other organisms, is presumably of great significance as a source of food.

Even in this region of high nitrogen content 2.88 cc. of Vineyard Sound water contained less than one-fifth the theoretical food requirement, and in all probability not over one-tenth this amount since half the nitrogenous matter is believed inassimilable, and some of the particles were probably too large or too small to be captured. Yet *Calanus* survives and grows in this region. Two explanations are

possible: (1) *Calanus* in nature requires less food than that calculated from laboratory experiments on oxygen consumption, or (2), *Calanus* in nature filters a greater volume of water and thus obtains more than the estimated amount of food.

### NUTRITIVE REQUIREMENTS OF CALANUS

Knowing the rate at which *Calanus* feeds on *Nitzschia*, it should be possible to supply the animals with known concentrations of

### TABLE V

*Survival and moults of Calanus fed on Nitzschia*

| Expt. No. | Nitzschia cells/cc. | Initial population | | Success-ful moults | Deaths in moult | Deaths not in moult | Percentage reaching moult | Average survival |
|---|---|---|---|---|---|---|---|---|
| | | No. | Stage | | | | | |
| B1 | 300,000 | 2 | III | 0 | 2 | 0 | 63.2 | *days* 8.9 |
| | | 12 | IV | 1 | 8 | 3 | | |
| | | 5 | V | 0 | 1 | 5 | | |
| B2 | 150,000 | 11 | IV | 1 | 3 | 7 | 33.3 | 9.7* |
| | | 4 | V | 0 | 1 | 3 | | |
| B3 | 30,000 | 14 | IV | 0 | 5 | 9 | 38.9 | 9.5 |
| | | 4 | V | 0 | 2 | 2 | | |
| B4 | 15,000 | 8 | IV | 0 | 3 | 5 | 41.1 | 10.4* |
| | | 11 | V | 0 | 5 | 5 | | |
| B5 | 0† | 10 | IV | 0 | 1 | 9 | 18.7 | 11.0* |
| | | 6 | V | 0 | 2 | 3 | | |
| B6 | Harbor water | 4 | IV | 0 | 3 | 1 | 60.0 | 7.2 |
| | | 16 | V | 0 | 9 | 7 | | |

* In each of these experiments one stage V still living after 19 days.
† All attempts to moult near end of experiment. Examination showed minute protozoa present. None in Experiments B1–B4.

diatoms, observe the minimum concentration at which growth takes place, and calculate the food requirement in terms of planktonic organic nitrogen. Experiments were set up in which 15 to 20 *Calanus* were placed in 250 cc. of Berkefeld filtered sea water containing definite concentrations of *Nitzschia*. The concentrations chosen together with the amount of nitrogen per cc. in each case were:

(B1)   300,000 cells and $0.27\gamma$N per cc. representing a concentrated food supply with the theoretical amount of nutriment contained in 2.5 cc.

(B2)   150,000 cells and $0.135\gamma$N per cc., half the above.

(B3)   30,000 cells and $0.027\gamma$N per cc. representing an approximation to the concentration of organic nitrogen found in Vineyard Sound.

(B4)   15,000 cells and $0.014\gamma$N per cc., half the above.

(B5)   Berkefeld filtered water—no diatoms.

(B6)   Water collected from Woods Hole Harbor.

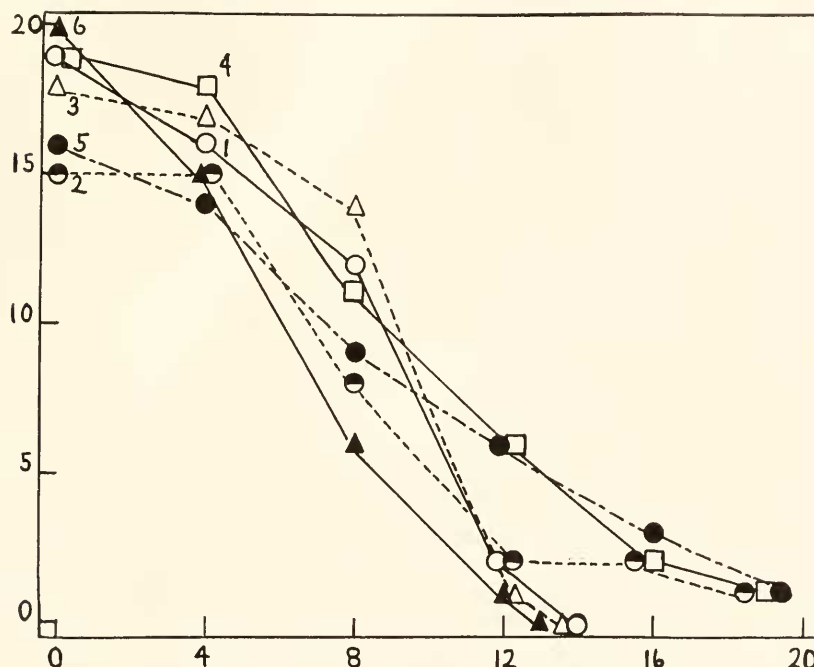The medium was changed daily except Sunday, and dead animals were removed at each observation period.   Animals were transferred



Fig. 2.   Series B.   Survival of *Calanus* fed on different concentrations of *Nitzschia*.   B1—300,000   cells/cc.;   B2—150,000   cells/cc.;   B3—30,000   cells/cc.; B4—15,000 cells/cc.; B5—Berkefeld filtered water; B6—water from Woods Hole Harbor.   Ordinates: *Number of survivors*.   Abcissæ: *Time in days*.

by means of a lifter of bolting cloth or in a wide-mouthed pipette. In order to study growth, stage IV *Calanus* were used insofar as they were available.   Survival was uniformly poor compared with experiments which were reported previously by Fuller and Clarke.[2]

These experiments are summarized in Table V and Figs. 2 and 3.

[2] Clarke and Zinn found that in both 1935 and 1936 there was a sharp reduction in the *Calanus* population in Vineyard Sound during the latter part of August.   The animals were either being carried away, or were dying off.   This may explain the high mortality in these experiments.

The previous observation that ecdysis is a critical period for *Calanus* is again brought out by the data for "deaths in moult." It is believed, however, that the attainment of the moulting stage represents true growth, and indicates that the animals are feeding, since ecdysis does not occur in starved animals (Fuller and Clarke, p. 312). If the attainment of the moulting stage—whether successful or not—be taken as the criterion, growth is most rapid in the most concentrated diatom suspension and in harbor water in which media 63.2 and 60 per cent, respectively, of the original population reached the moulting stage. Growth rates in the other diatom suspensions are essentially equal
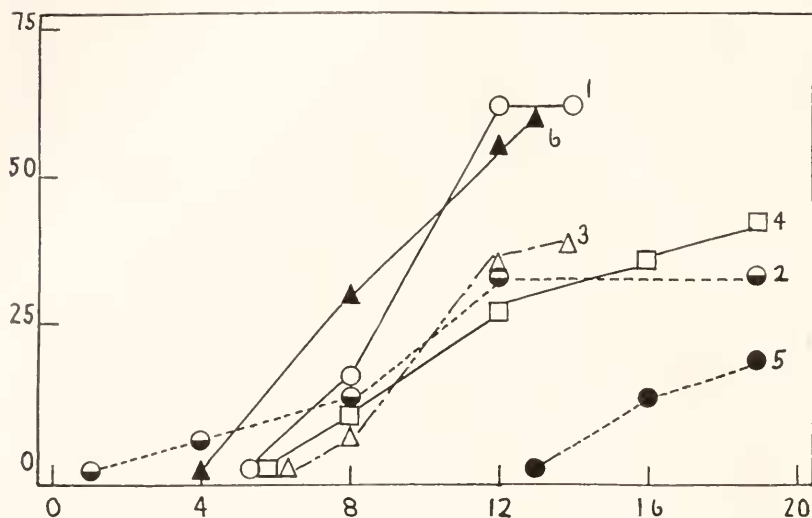


FIG. 3. Series B. Percentage of original population of *Calanus* attaining moulting stage when fed different concentrations of *Nitzschia*. Symbols as in Fig. 2. Ordinates: *Percentage of moults.* Abscissæ: *Time in days.*

(33–41 per cent), while the few moults which occurred in Berkefeld filtered water (19 per cent) are probably due to a protozoan infection of the culture which developed during the last few days of the experimental period and furnished a food supply for the copepods. There is a definite negative correlation between the average survival period in each experiment and the percentage of animals attaining the moulting stage. This is attributed to the fact that when growth is slower, the critical period of moulting is reached later and average survival increases.

If each *Calanus* captured daily the diatoms from 2.5 cc. of water, then in Experiment B4 in which some growth obviously took place, each individual obtained per day only 37,500 cells, $0.034\gamma N$, and

between 8 and 16 per cent of the food requirement calculated from oxygen consumption. The higher value assumes all the nitrogenous matter to be utilized; the lower value is based on the assumption that one-half is utilized.

## DISCUSSION

The filtering rate of *Calanus* in these experiments was less than that found by Fuller and Clarke using carmine particles, the previous value at 13° C. being 5.61 cc. per day against 1.09 cc. reported above. As the carmine particles tended to settle and were more difficult to count, the present values are the more reliable. Harvey (private communication) has found filtering rates of from 50 to 100 cc. per day using the larger diatoms *Lauderia* and *Ditylium*, though his values are based on only a few experiments. It seems probable that large particles are captured more readily, though the carmine particles mentioned above were somewhat smaller than *Nitzschia*.

Whether these varying results represent actual differences in the rate of filtering is a moot point. Possibly the variance depends upon the efficiency with which the maxillary bristles strain out particles of different sizes and shapes. It may be that small cells, such as *Nitzschia*, pass between the bristles so that a copepod retains only a small percentage of the *Nitzschia* in the water current which it generates. This is the author's view. On the other hand some investigators believe that copepods possess other food-capturing mechanisms besides filtration.

Lowndes (1935), basing his opinion on anatomical grounds, and on observation of living unrestrained animals, states that feeding of the calanoid copepods cannot be merely automatic, non-selective filtering, but involves the finding and grasping of food particles. *Calanus* has two distinct types of movement: (1) saltation in which propulsion is furnished by the antennules and swimming feet, and (2) a slow glide in which the motive force comes from the vibration of the mouth parts. It is the latter which furnishes the feeding current. Often this species remains suspended quietly in the water for several minutes. Since the eye of copepods is not capable of forming images, recognizance of food material would have to be chemical or tactile in nature. In a turbulent fluid medium, only tactile stimuli would be serviceable in precisely locating food. Saltations might enable a copepod to try out different regions for food, the filtering mechanism being called into play only when food was encountered. One would thus expect more filtering where food was abundant since more particles would be encountered. On the other hand, the rate of feeding might be controlled by the amount of food ingested, so that filtering would slow

down when food was abundant and speed up when food was scarce.
No tendency towards a change in the filtering rate was shown. Har-
vey's results agree in this respect. Two conclusions are possible: (1)
the rate of filtering is independent of the amount of food ingested or
encountered; (2) even in the highest diatom concentrations used in
these experiments there was insufficient food so that filtration was
maintained at a maximal rate. Since in many experiments (e.g.
7 and 8) diatoms were present in concentrations much higher than are
ever found in nature, alternative (2) is ruled out. The evidence
definitely favors the theory that filtration is an automatic process
independent of the concentration of food, though its rate is modified
by physical factors in the environment.

These factors insofar as they have been studied may be considered
in relation to the ecology of the species. The suggestion of a diurnal
feeding rhythm is nicely correlated with the habit of vertical migration
in this species which rises to the surface at night, and sinks below this
rich food zone during the day. Neither phenomenon is absolutely
regular. Probably both are dependent upon the physiological state
of the animal which conditions its response to light (see Clarke, 1934).
The ability of *Calanus* to feed at temperatures as low as 3° C. and its
high rate of filtering at 8° indicate a physiological adaptation to life
in the colder parts of the ocean.

The question of the food requirement of *Calanus* is perhaps of
greatest fundamental importance, since the rôle of the food supply in
the regulation of the *Calanus* population can only be determined when
the minimum requirements for metabolism and growth are known.
The discrepancy between the requirement calculated from oxygen
consumption measurements and that estimated from measurements of
the filtering rate and the concentration of particulate matter in the sea
has been mentioned above.

It was hoped that the experiments of Series B reported herein would
resolve this difficulty, but the heavy mortality occurring in them makes
definite conclusions unsafe. However, a higher percentage of copepods
attained the moulting stage in Experiment B4 with a minimum con-
centration of diatoms, than in Experiment B2 with ten times as many,
although there was one successful moult in the latter experiment
against none in the former. Presumably each copepod in Experiment
B4 received not over one-sixteenth of the food requirement calculated
from oxygen consumption. It is unlikely that the filtering rate in
B4 was sixteen times greater than in any of the experiments in which
the rate was measured. Thus it is probable that the minimum
nutritive requirement for growth is less than previously believed,

though it is as yet impossible to set a definite figure. Why higher concentrations of food have so little effect on the rate of growth is problematical unless the concentration in B4 itself is well over the required minimum. Another problem is the reason for the rapid growth of *Calanus* in harbor water. Possibly qualitative as well as quantitative differences in the food supply are involved in this case.

When larger particles serve as food the effective filtering rate is probably higher. If so, the concept of the feeding rate taken at the beginning of this work—namely the volume of water filtered per unit of time—must be modified. Instead the feeding rate must be considered as the number of particles of a given type captured per unit of time when present in a given concentration.

It follows that the investigation of the minimum concentration of food which will support life and growth in *Calanus* and in other species must employ several types of food organisms. The problem is a complex one, for it is possible that the metabolic rate of *Calanus* varies with the amount of food taken in as well as with other environmental factors.

## Summary

(1) The filtering rate of *Calanus finmarchicus* on the diatom, *Nitzschia closterium*, was measured under different conditions of diatom concentration, light and temperature, by observing the reduction in concentration of the diatoms. Change in diatom concentration had no effect on the rate of filtration. There was some evidence of a diurnal feeding rhythm with greater activity at night. Feeding was most rapid at 8° C., slower at 13° and 3°.

(2) Studies on the growth of *Calanus* supplied with different concentrations of diatoms indicated that the food requirement is less than has been calculated from oxygen consumption measurements. This is also borne out by comparing the amount of particulate organic matter in the sea with the rate of feeding measured in the laboratory.

(3) The view that the feeding activity of *Calanus* is automatic filtering is favored by these experiments.

(4) Approximately one-half the organic nitrogen content of *Nitzschia* is in a form available to *Calanus*.

(5) These results are correlated with the ecology of *Calanus* as studied in the field.

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